HOST-PARASITE RELATIONS AND EVOLUTION
OF THE METASTRONGYLOIDEA (NEMATODA)

BY

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GENERAL

The Metastrongyloidea is a rather small nematode superfamily of the Strongylida consisting of about 180 species classified into about 45 genera and 7 families (Anderson, 1978). The superfamily is, like the Ancylostomatoidea, confined to mammals. Metastrongyloids are commonly associated with the respiratory system and this has led to the name "lungworms". Some genera, however, are associated with lymph or blood vessels far removed from the lungs and a few genera occur in nasal sinuses and Eustachian tubes. Typically, however, larvae leave the host via the bronchial escalator and the alimentary tract.

HOST DISTRIBUTION

Metastrongyloids are most diverse in Artiodactyla (13 genera), Carnivora (14), marsupials (7) and Cetacea (Odontoceti) (6). A few genera are restricted to insectivores (5), rodents (3) and primates (10.) Lagomorpha share a genus (*Protostrongylus*) with artiodactyls. Obviously absent as hosts are such major groups as Chiroptera, Edentata, Mysticeti, Proboscidea, Hyracoidea and Perissodactyla. There is considerable evidence many lungworms exhibit a high degree of host specificity in the final host.

Metastrongylidae : The family contains only *Metastrongylus* found in Suidae. No species is reported from Tayassuidae and Hippopotamidae. In this genus the six primitive lips are fused into lateral trilobed structures and the first-stage larva remains in a thick-shelled egg until ingested by terrestrial oligochaetes which serve as intermediate hosts.

Protostrongylidae : The family contains some 12 closely related genera distributed among Bovidae, Cervidae and Antilocapridae ; it is unrepresented in Giraffidae, Tragulidae and Camelidae. The most distinctive features of the group are the complex gubernaculum and telamon (Boev, 1975). Almost half (29) of the known species of the Protostrongylidae fall within the genus *Protostrongylus*. In addition, the latter is the only genus with species in lagomorphs. The family basically parasitizes ruminants and apparently has secondarily adapted to lagomorphs.

Crenosomatidae : The family includes five closely related genera in the bronchi of insectivores and carnivores, the nasal sinuses of marsupials (*Didelphis*) and the bronchi and veins of pinnipeds.

Angiostrongylidae : The Angiostrongylidae has about 16 genera and approximately 48 species with a wide geographic distribution in marsupials, insectivores, carnivores and rodents. The group requires more study. It includes a number of tiny species, difficult to extricate from the host and difficult to study. There is, therefore, much room for differences of opinion as to affinities and the status of genera.

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The six primitive lips are highly developed in some genera in marsupials and insectivores (*Madangiostrongylus*, *Didelphostrongylus*, *Heterostrongylus*) and we suspect these are primitive. However, *Filostrongylus* and *Marsupostrongylus* of Australian marsupials have greatly reduced lips and obvious affinities to forms in insectivores, rodents and carnivores (Spratt, 1979). The group seems so discontinuous in morphologic detail that one wonders if many forms remain to be discovered.

There is within the Angiostrongylidae, an obvious tendency towards bursal reduction leading to such genera as *Madafilaroides* of insectivores (*Tenrec*) and *Andersonstrongylus* of mustelids which link the family to the abursate Filaroididae.

Filaroididae : The family contains three genera in which the bursa is atrophied (Webster, 1978). *Filariopsis* of primates retains vestigial rays but even these vestiges are lost in *Oslerus* of canids and felids and *Filaroides* mainly of terrestrial carnivores and pinnipeds. The family has obviously been derived from ancestors resembling some present day Angiostrongylidae (see Dougherty, 1949). That the family is extremely ancient is indicated by the fact that species of *Filaroides* occur in Australian marsupials (Spratt, 1979).

Skrjabingylidae : The family is represented by the single genus *Skrjabingylus* with about six species found in frontal sinuses of Mustelidae. The skrjabingylids seem to be an ancient remnant group which has survived by isolating itself in a special site in the host leaving the lungs to forms represented by the Angiostrongylidae and Filaroididae.

Pseudaliidae : The Pseudaliidae, with 7 genera and about 23 species is restricted to the toothed whales (*Odontoceti*) with the exception of *Stenuroides* of Viverridae (*Herpestes*) (Arnold and Gaskin, 1975). The group displays profound bursal modification, including, unique fusion of rays.

LIFE CYCLES

The metastrongyloids are basically heteroxenous. Most life cycles studied show that terrestrial gastropods are intermediate hosts in which development to the third infective stage takes place. Exceptions are (1) *Metastrongylus* of swine which utilizes earthworms ; (2) *Filaroides* (*Parafilaroides*) *decorus* of Otariidae which utilizes coprophagous fish ; and (3) certain highly specialized Angiostrongylidae (e.g. *Andersonstrongylus*) and Filaroididae (e.g. *Filaroides hirthi*, *Oslerus osleri*) in which first-stage larvae are infective. We assume the absence of heteroxenity is a secondarily acquired feature and that heteroxenity is basic and primitive in lungworms because of its widespread occurrence throughout the various families (life cycles of Pseudaliidae are unknown, however).

Heteroxenity within lungworms is of three types.

Type I : The intermediate host is an essential item in the diet of the final host. This is probably the primitive mode of transmission. It is probably found mainly among lungworms of insectivores, rodents and a few of the smaller carnivores.

Type II : The intermediate host is accidently ingested with food of the final host. This mode of transmission depends upon the host consuming large quantities of ground vegetation. This type of transmission occurs among lungworms of ruminants and lagomorphs.

Type III : A paratenic or transport host is placed between the intermediate and final hosts. The paratenic host feeds on gastropods and is itself a consistent part of the diet of the final host. Paratenesis is undoubtedly a common feature of lungworms of terrestrial carnivores. It may also be a feature of the transmission of the Pseudaliidae although some form of Type I mode of transmission may also occur.

There is a striking similarity in development of metastrongyloids in the intermediate host, regardless of the taxonomic position of various species. For example, the infective stage has a buccal cavity which is immediately distinctive of the metastrongyloids. This raises the possibility that heteroxenity is extremely ancient in the group and that there are genuine affinities between lungworm families even though evolution has often brought about some rather radical changes in adult forms.

Paratenesis involves the ability of infective larvae to withstand defence mechanism which would normally overcome parasites in other than the final host. In the metastrongyloids, paratenesis must have had a considerable period of evolution. It would arise in response to shifts in food preferences of final hosts from molluscs to prey vertebrates which themselves continued to consume gastropods consistently e.g. certain insectivores, rodents, reptiles and amphibians. It was probably crucial for the survival of many groups of lungworm during the radiation of carnivores from unspecialized ancestors. Initially, larvae in secondary hosts would tend to be overcome in the tissues. Some larvae would survive, however, and he passed to the definite host. In this way a process of selection could become established leading to strains of parasites capable of surviving as infective larvae for increasingly prolonged periods in secondary hosts. The evolution of paratenesis would have gone hand in hand with the specialization of predacious hosts until transmission would normally he achieved through this mechanism.

THE CONSEQUENCES OF HETEROXENITY

Metastrongyloids departed from the stem which gave rise to other hursate superfamilies hy (1) colonizing an organ system not utilized extensively by the ancestors of the Trichostrongyloidea, Strongyloidea and the Ancylostomatoidea and (2) by developing heteroxenity which tied transmission closely to feeding hehaviour of the host. We presume that ancestors of lungworms were once widespread in ancient unspecialized omnivorous mammals which utilized terrestrial invertebrates as food, including molluscs and earthworms.

The development of heteroxenity prohably had momentous consequences for lungworms. It would have led to the extinction of many groups in mammals which developed certain specialized feeding hahits. It would have allowed for the development of paratenesis and adapted some lungworms to more specialized hosts (e.g. many modern carnivores). It would have allowed some groups to adapt to some strictly aquatic mammals, something the monoxenous hursate superfamilies never achieved:

The absence of lungworms in many major mammalian groups may he related to the highly specialized feeding patterns which evolved within mammals. For example, it is scarcely surprising to find lungworms absent in Chiroptera, Proboscidea, Giraffidae and Edentates. Horses are, in contrast to many Bovidae, extremely particular in their feeding habits and are unlikely to ingest gastropods with their food. Such peculiarities might have eliminated lungworms from some major groups of mammals.

Nematodes of strictly aquatic vertebrates are rarely monoxenous ; a few exceptions are found among oxyuroids of tadpoles which congregate in shallow water making contaminative transmission and monoxenity feasible (Adamson, 1981). We assume, therefore, that lungworms had a terrestrial origin and heteroxenity and later paratenesis evolved under terrestrial conditions. Parasites which developed heteroxenity and paratenesis under terrestrial conditions could have adapted to aquatic systems with their hosts provided a high degree of specificity had not yet evolved. The adaptation to aquatic intermediate and paratenic hosts in the food chain of the final host would ensure their survival. We helieve this accounts for the presence of lungworms in certain Pinnipedia and Cetacea. Monoxenous parasites could never make this transfer and are therefore absent in strictly aquatic mammals.

Evolution of Otariidae and Phocidae from terrestrial carnivores (Repenning, 1980) explains the presence of *Filaroides* (*Parafilaroides*) in hoth families (Dailey, 1975). Ancestors of these lungworms probably occurred widely in terrestrial carnivores hefore the appearance of the Pinnipedia ; *Filaroides* (*Filaroides*) and related genera are widespread in modern carnivores, especially mustelids and canids. Thus, although the ancestry of otariids and phocids may differ (Repenning, 1980), their lungworms may have had a common origin.

Altbough *Otostrongylus* (Crenosomatidae) is found only in Phocidae, allied genera (*Crenosoma*

and *Troglostrongylus*) are common in mustelids, ursids, felids and procyonids, again showing links between pinnipeds and terrestrial carnivores.

The Pseudaliidae is unquestionably extremely ancient. The occurrence of one genus in Viverridae suggests a relationship between Odontoceti and carnivores but it is more likely a matter of convergence. The ancestors of pseudaliids probably occurred in the terrestrial ancestors of the cetaceans. Pseudaliids have probably persisted because more modern competitors could not arise in the strictly aquatic niche taken up by their hosts. Elucidation of the life cycles of the pseudaliids may help to explain their apparent absence in the Mysticeti. One suspects that food habits of these cetaceans (Gaskin, 1976) may be involved.

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DISCUSSION

WERTHEIM. — Have enough animals been examined to be sure lungworms are absent in some of the groups you mentioned ?

ANDERSON. — Lungworms are often pathogenic and it is doubtful if they have been overlooked in such groups

as giraffes and horses. Also, they should be easy to find in bats. Still, it is possible that some species have been overlooked in some groups mentioned.

EUZET. — Dans le cycle de ces Nématodes, quel est l'hôte primitif ? Pensez-vous que le cycle évolutif des ancêtres des Métastrongylides s'effectuait entièrement chez les Mollusques ?

ANDERSON. — No. I agree with M. Chabaud that the intermediate host is a recent acquisition. Otherwise it would be impossible to account for the affinities of the bursate superfamilies. The agreement that the lack of specificity in the mollusc intermediate host indicates a recent association may not be valid because it might he biologically advantageous to have a wide range of intermediate hosts rather than a narrow range.

SCHAD. — Now that we know of three species of metastrongyles infective in the first-stage is it not possible that other species which we believe require an intermediate host might not require it ? It seems that since the work of Hobmaier it has heen assumed that the third stage in the molluscs is the infective stage.

ANDERSON. — Yes. I suppose a few other examples will he found. However such life cycles must be atypical. They occur as far as we now known only in very specialized Angiostrongylidae and Filaroididae. We must keep an open mind but such life cycles depart from the rule of the third infective stage in the secernenteans and I think we are justified in regarding them as atypical.

MAS-COMA. — In our studies on small mammals we have seen that some metastrongyloids are only found in specific hosts (e.g. *Stefanskostrongylus soricis* in *Sorex minutus* in Europe, *Gallegostrongylus ibicensis* in *Mus* on the island of Ibiza). Do you think metastrongyloids are so specific in the sense of a specificity *sensu stricto* (biochemical of physiological) as to be able to distinguish between species of the same host genus or proximal host genera, or is it a result of differences in host diet ?

ANDERSON. — We require much more experimental evidence to he sure. My own impression is that the lungworms of mustelids, for example, are highly host specific in the physiological sense.

SPRENT. — Your group would seem to lend itself, because of their location in the host, to surgical transfer to determine whether their apparent specificity has a physiological or hiochemical basis. For example, you could transfer *Skrjabingylus* from a skunks sinuses to a civet-cat's sinuses and observe its behaviour and growth in different hosts. Has any work been performed along these lines ?

ANDERSON. — Very little. We know that normally skrjabingylids reach the sinuses hy migrating in the vertebral canal and across the hrain. We also know that it is possible to infect kids with *Parelaphostrongylus tenuis* hy putting the infective larvae into the peritoneal cavity. In this case the larvae are behaving as they would in the usual host. Some work has also been done with *Angiostrongylus cantonensis*. A concerted effort to study lungworms by these methods might he useful.

KAUSE. — You have indicated that lungworms may be highly specific in the final host but this is not necessarily true in the genus *Metastrongylus* in which the species are capable of occurring in a wider range of hosts than previously thought.

ANDERSON. — I was speaking generally. *Metastrongylus* is atypical in several ways. Nevertheless, I must admit that we really do not know enough about host specificity in lungworms. It is often difficult to distinguish physiological specificity from ecological specificity in the absence of experimental evidence.

INGLIS. — In response to some questions you seem to have said that the parasite is " unusual " or " atypical ": Can you tell us which parasites you consider " usual " and why ?

ANDERSON. — I think I used the term first in reply to question about species with direct life cycles. I call these worms atypical or specialized because morphologically they have greatly reduced hursae (e.g. *Andersonstrongylus*) or are, in fact, abursate (e.g. *Oslerus*, *Filaroides*). Thus, both in their morphology and life cycles, they depart from the usual pattern found in the metastrongyloids. Similarly *Metastrongylus* is a rather atypical member of the superfamily, for example in its use of earthworms as intermediate hosts.